ON THE ANATOMY AND EMBRYOLOGY OF THE NERVOUS SYSTEM OF THE SCORPION.[1]

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Early in May, 1903, at the suggestion of Dr. William Morton Wheeler, at that time professor of zoölogy in the University of Texas, I began collecting females and preserving embryos of the scorpion here considered. I found the scorpions under stones on certain hills covered with scrub oak, scrub cedar or grass in the neighborhood of Austin, Texas. They prefer dry areas with an abundance of broad, flat stones, or at least stones lying loosely on the ground, under which they hide. The first scorpions collected (May 13) contained eggs in early cleavage stages, and the last scorpions taken that year, June 10, contained embryos with pigment well developed in the eyes. The next year the scorpions developed earlier, and by the first of June I procured successive stages of the embryo up to the time of birth. Most of the work was done at the University of Texas during the session of 1903–04, under the direction of Dr. Thomas H. Montgomery, professor of zoölogy.

Material and Methods.

The species of scorpion I worked on is that described and figured by R. J. Pocock in the Biologia Centrali Americana under the name of *Centrurioides vittatus* Say. I sent some specimens to Professor Kraepelin, and he identified them as *Centrurus infamatus* C. L. Koch. This is probably synonymous with *Scorpio carolinianus* Palisot de Beauvois, and probably the species Patten (1890) worked on, *Buthus carolinianus*, as stated in his paper.

The embryos, either in the ovarian tubules or dissected out, were fixed in Lee's picro-acetic, Kleinenberg's picro-sulphuric, or Tower's alcohol-corrosive-aceto-nitric (*Zoöl. Jahr. Anat. Ontog. d. Thiere*, Vol. 17, heft 3, 1903). As all the embryos taken from one mother are in the same stage of development it is convenient

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to keep them in a separate vial. The embryos may be studied in alcohol, but for cleared preparations the following process was found to give good results: The yolk was removed with needles and fine brushes and the embryos were then stained in Delafield's hæmatoxylin, diluted with water acidulated with a trace of picro-sulphuric, dehydrated with alcohols acidulated with the same and mounted in balsam. The intensity of the stain must be controlled by the proportions of the stain and acid used, and the time they are allowed to act. Eggs for sectioning were imbedded in paraffin and the block cut so as to remove as much of the yolk as possible without injury to the parts desired, then re-imbedded and sectioned and stained in Heidenhain's iron-hæmatoxylin. It is difficult, even with the use of the mastic-collodion process, to obtain perfect series of the entire egg. Embryos ready to hatch could be to some extent dissected, but contained a large amount of yolk.

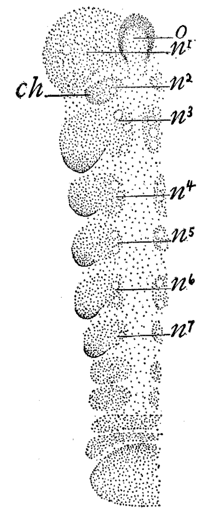


FIG. 1. Camera lucida drawing of the right side of a cleared surface preparation of the embryo of *Centrurioides vittatus* as early as the neuromeres are clearly distinguishable, × 45. *ch*, chelicera; n^{1-7}, first to seventh neuromeres; *o*, mouth.

Adults for dissection were opened while fresh and the blood washed out and liver partly removed in physiological salt solution, then hardened in weak alcohol. Adults for sectioning were taken immediately after moulting and injected with Flemming's fluid, in which they were left six days, followed by pyroligneous acid (v. Mährenthal), or pyrogallic acid (Hermann) for two or three days; or they were stained with Heidenhain's iron hæmatoxylin after any good fixative. This latter process brings out the nerve-fiber tracts in the fibrous substance of the nerve center. In staining on the slide, parts of sections were often washed off, though they had been attached with Meyer's albumen fixative, flattened with the aid of warm water, and dried for twenty-four hours. To prevent this I took the slides after drying and painted them with three fourths per cent. celloidin (Gage) and

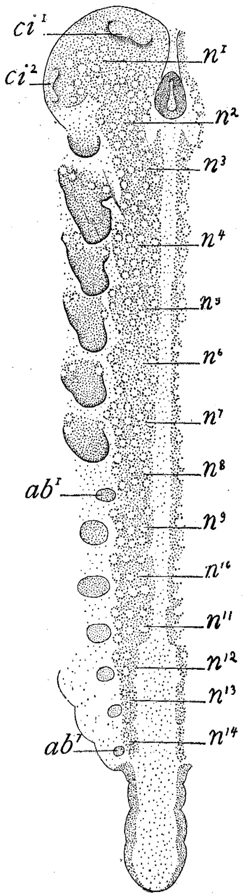


FIG. 2. Second stage of same, $\times$ 45. The post-abdomen is turned under to show the posterior neuromeres. ab^{1-7}, first to seventh abdominal appendages; ci^1, first cerebral invagination, to join later with its fellow of the opposite side to form the semi-lunar lobe; ci^2, second cerebral invagination; n^{1-14}, first to fourteenth neuromeres.

dried them again. After this treatment no sections came off unless they were left too long in absolute alcohol.

HISTORICAL.

As early as 1870, Metschnikoff represented the neuromeres as paired thickenings of the ectoderm on surface views of the scorpion embryo, there being one neuromere for the segment bearing the eyes, one for the segment bearing the chelicera and so on for succeeding segments back to the point where the fold of the post-abdomen hid them from view. A "longitudinal furrow" runs from the mouth backward, separating the two halves of each neuromere. His figures show also the relation of the anterior neuromeres to the mouth — that is to say the mouth is formed in the first segment and during development moves to the posterior part of the second segment, by which process the second neuromere becomes pre-oral.

Kowalevsky and Schulgin (1886) described the transformation of undifferentiated ectoderm into nervous tissue. The ectoderm, in the regions of the future ganglia, begins to thicken and the cells to increase in number rapidly and minute pits are formed all over its free surface. These pits are gradually filled up by the growth of the cells forming their walls. This method of cell increase and growth was supposed by the writers to possess peculiar advantages. Unfortunately they gave no figures.

Saint-Remy made a comparative study of the "brains" of different groups of air-breathing arthropods, which he published in

several papers, the last of which (1887) contains the results of all his work on the subject. He worked out the nerve cell-groups and the nerve fiber-tracts and came to the conclusion that there are *two* pre-cheliceral neuromeres in the scorpion. But his observations do not seem to support his conclusions, for, while he showed that there are, corresponding to these two neuromeres, two pairs of optic lobes, he described their nerve-fiber tracts communicating with the interior of the "brain" as united to form one. He showed great complexity in the structure of the "brain."

In 1890, Patten, in a preliminary paper on the origin of vertebrates from arachnids, compared the arachnid cephalothoracic nerve mass, or "brain," with the vertebrate brain, turning the former up-side-down in order to get the proper relation with the digestive tube. In the scorpion embryo he found three precheliceral neuromeres, each with a pair of optic ganglia. In each optic ganglion was an invagination. The cephalo-thoracic nerve mass was composed of thirteen neuromeres. In the adult, a typical neuromere had a pair of "neural" nerves and two

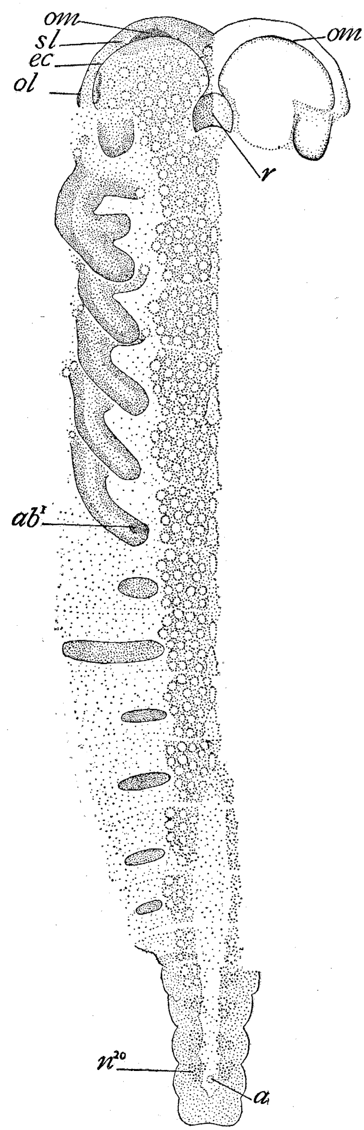


FIG. 3. Third stage of same, $\times$ 45. On one side the head is represented as an opaque object. *a*, anus; *ab*1, first abdominal appendage; *ec*, anterior margin of the ectoderm growing over the first neuromere; *n*20, twentieth neuromere; *ol*, ectodermal thickening to form the lateral eye; *om*, ectodermal invagination to form the median eye sac; *sl*, semilunar lobe; *r*, rostrum.

pairs of "hæmal" nerves, and each neural nerve had a ganglion at its base. The first neuromere was nerveless; the second had a pair of neural nerves to the median eyes and a pair of hæmal nerves to muscles; the third neuromere had a pair of neural nerves to the lateral eyes and two pairs of hæmal nerves to muscles; neuromeres four to nine had each a pair of neural nerves to appendages and two pairs of hæmal nerves to internal muscles. The last four neuromeres had their neural nerves all united into one pair, that innervated the pectines, but each had two pairs of hæmal nerves which went to make up a system homologous to the vagus nerve of vertebrates. In each of the neuromeres succeeding the "brain" there was one pair of neural nerves, and only one pair of hæmal nerves well developed. These two pairs of nerves united a short distance from the nerve center to form a single pair homologous to spinal nerves of vertebrates. Patten figured the pits that form in the neuromeres in the early embryonic stages, and he supposed that they represented sense-organs from which the nervous system arose. In the course of development a piece is constricted off of each ganglion of the ventral chain in each segment and added to the succeeding ganglion.

Viallanes' work (1893, 2) was chiefly on *Limulus* and does not bear directly on our subject, but it is interesting to note that he held the view that there is only one pre-cheliceral neuromere in the arachnid type of nervous system.

Braner (1894–5) worked out the earlier half of the embryology of the scorpion. He clearly described and figured the early development of the eyes and their relation to the nervous system, a matter that had been confused by all previous workers on the subject. He supported Kowalevsky and Schulgin's explanation of the pits in the embryonic nerve tissue, rather than Patten's. The ectoderm was found to grow over the ventral chain from the sides. Brauer reckoned the number of neuromeres by the cross-commissures, there being two in front of the cheliceral segment. But it is not evident why he should count cross-commissures rather than nerves or ganglia, which are equally characteristic parts of a neuromere. Such a criterion for neuromere would hardly be accepted in a form like *Peripatus*.

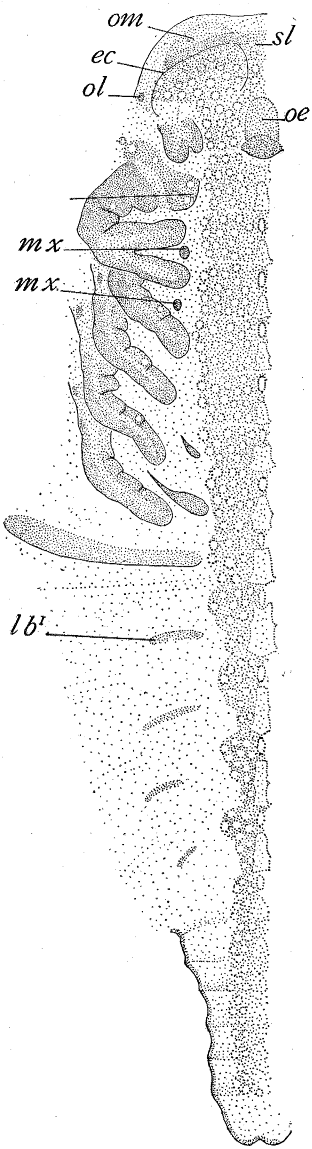
Laurie (1896, 1 and 2) described the variation in positions of the abdominal ganglia in different species of scorpion.

Police described the anatomy of the nervous system of the scorpion (1901, 1) and the histology of the subintestinal portion (1901, 2). He described the typical neuromere as a pair of ganglia fused in the mid-line and giving off two pairs of nerves, "external" and "internal." The longitudinal connectives continue through the fibrous substance of the nerve center as a pair of "central columns," which are connected by two tracts of commissural fibers, anterior and posterior. There is also a pair of "ventral columns." The central columns send nerve fibers into both pairs of nerves, those going into the internal nerves leaving the columns at the posterior cross-commissure. The ventral columns send nerve fibers into the external nerves. This classification of the nerves as "external" and "internal" is unfortunate, for, although in some abdominal neuromeres the external nerves do arise from a broader part of the nerve center than the internal, and are properly described by the name, in the thoracic neuromeres they do not. They had better be described as anterior and posterior, since during the early embryology they all conform to this description.

Lankester (1904) held the view that there is only one precheliceral neuromere.

Descriptive.

Stage 1.—(Fig. 1.) This is the earliest stage in which the neuromeres can be clearly distinguished from the rudiments of the appendages. In addition to the telson, which is not considered as a segment in the strict sense of the term, eleven segments have been formed. Appendages are appearing on segments two to seven. Neuromeres can be distinguished on segments one to seven, being represented by paired thickenings of the ectoderm indented with small pits. The first neuromere, composed of a pair of "cephalic lobes," is much larger than any of the others. The oral invagination (*o*) is appearing in the first segment. From the mouth backward to the tenth segment in this stage is a median depression, the longitudinal furrow of Metschnikoff or median furrow of Patten. The depression is caused by the ectoderm being thinner in this region.



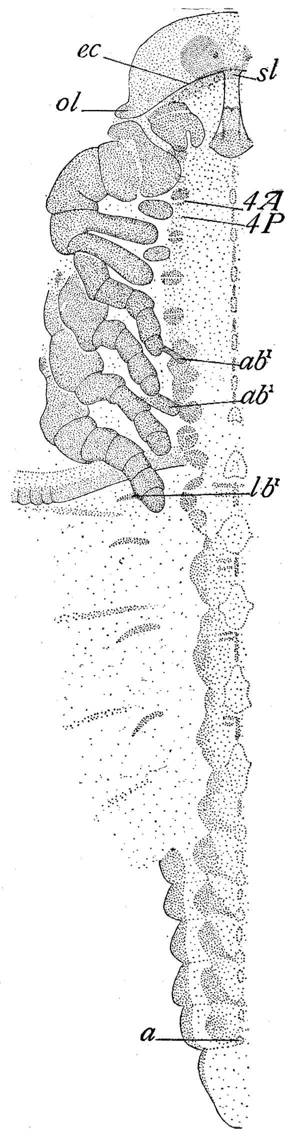
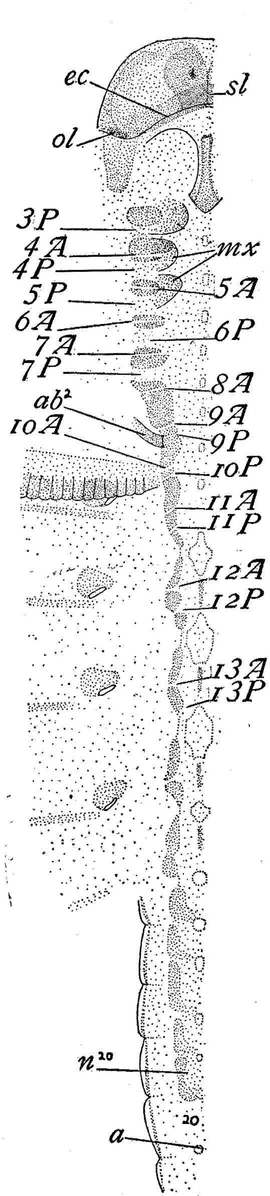


FIG. 4. Fourth stage of same, × 45. *ec*, anterior margin of ectoderm growing over the first neuromere; *lb*¹, first lung book; *mx*, maxillaria; *œ*, œsophagus; *ol*, latera-eye; *om*, median eye sac; *sl*, semilunar lobe.

FIG. 5. Fifth stage of same, × 45. *a*, anus; ab^{1-2}, first and second abdominal appendages; *ec*, anterior border of ectoderm growing over first neuromere; *lb′* first, lung book; *ol*, lateral eye; *sl*, semilunar lobe; 4*A*, anterior nerve of the fourth neuromere 4*P*, posterior nerve of fourth neuromere.

Stage 2. — (Fig. 2.) Seventeen segments have formed. Appendages are present on segments two to fourteen and neuromeres in segments one to fourteen. The median furrow is continued backward and is very broad in segments twelve to fourteen, a condition probably due to the pressure of the post abdomen, which is turned under the pre-abdomen during the development of the embryo and not straightened out as shown in the figure. In addition to the numerous pits two pairs of invaginations have appeared in the first neuromere (ci^1, ci^2). These invaginations, while larger than the pits, are probably similar to them physiologically, for like them they are only temporary structures, being finally filled up by the growth of the cells forming their walls. Pits like those in the neuromeres have formed, externally and internally at the bases of the thoracic appendages and probably represent sense organs, as Patten maintains. It is not probable however that the pits in the neuromeres represent sense organs, since the embryology of the scorpion is of so specialized a type that we would not expect to find such remotely ancestral structures repeated here, when not repeated in more generalized types. The mouth has begun to move backward. This is accomplished in two ways : First there is an actual displacement, the ectoderm surrounding the mouth being thin and probably offering little resistance ; second, the mouth opening elongates and the anterior portion closes by the growing together and fusing of the two sides, the remaining opening being further back than the center of the original opening. The closure of the anterior portion of the mouth forms a lip called the rostrum (Fig. 3, *r*). It is thought by some that the rostrum represents the fusion of a pair of appendages. That it is formed by *fusion* is clear, but the only evidence I see in favor of regarding it as derived from *appendages* is the fact that in the later embryo and the adult it is innervated by a special nerve (Fig. 8, *R*). This nerve innervates the muscles of the anterior part of the œsophagus, or pharynx, also and might as well be called a pharyngeal as a rostral nerve.

Stage 3. — (Fig. 3.) Twenty segments, the complete number, have formed, and neuromeres are present in all of them. In the anterior part of each of segments three to twelve an elliptical



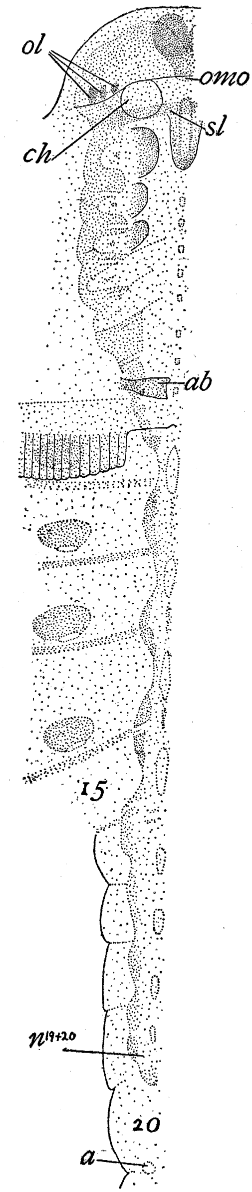


FIG. 6. Sixth stage of same, $\times 45$. The cephalo-thoracic appendages have been removed. Some of the details have been filled in from a study of serial sections. *a*, anus; ab^2, second abdominal appendage; *ec*, anterior border of ectoderm growing over first neuromere; *mx*, maxillaria; n^{20}, twentieth neuromere; *ol*, lateral eye; *sl*, semilunar lobe; 4–13*A*, anterior nerves of fourth to thirteenth neuromeres; 3–7, 9–13*P*, posterior nerves of corresponding neuromeres; 20, twentieth body segment.

FIG. 7. Seventh stage of same, $\times 45$. Cephalothoracic appendages removed; *a*, anus; ab^2, second abdominal appendage; ch^1, articulation of the chelicera; n^{19+2}, fusion of the nineteenth and twentieth nerve centers; *ol*, lateral eye; *omo*, common neck of the two median eye sacs; 15–20, fifteenth to twentieth body segments.

invagination is forming in the median furrow. The tissue thus invaginated is destined to form nerve tissue connecting the two halves of the neuromere in each of the segments mentioned. The process is carried backward to the posterior segments in later stages (Figs. 4, 5). These invaginations have the same appearance as the numerous pits so characteristic of the nerve tissue, differing from the latter however in time of appearance and in shape. The elongated shape is probably due to the narrowness of the median furrow. More pits are constantly being added to the neuromeres, and the late appearance of those in the median furrow is more apparent than real. In no case have I observed the invaginations of the median furrow to coalesce and form a temporary central canal, as Patten claims to have seen. The walls of the first pair of invaginations in the first neuromere have thickened and are fusing in the mid-line to form the semi-lunar-lobe of Patten (*sl*). The ectoderm has begun to grow backward over the first neuromere, its free border being shown at *ec*. On each side there is an invagination in the ectoderm close to the free border, forming the median-eye-sac (*om*), and an ectodermal thickening, to form the lateral eyes (*ol*). The ectoderm has begun to grow over the ventral chain from the sides, but this is not shown in the figure. Patten describes three pairs of ganglionic invaginations in the "cephalic lobes" the first of which I have represented in Fig. 2, ci^1, and Fig. 3, *sl*. The second, he describes in relation to the median eyes. I was unable to find it, either in sections or surface views. It is most probable that he referred to the ectodermal invagination or median eye sac (Fig. 3, *om*). The third he describes in relation to the lateral eyes and I have represented it in Fig. 2, ci^2; it may be seen also in Fig. 3 near the lateral eye rudiment (*ol*).

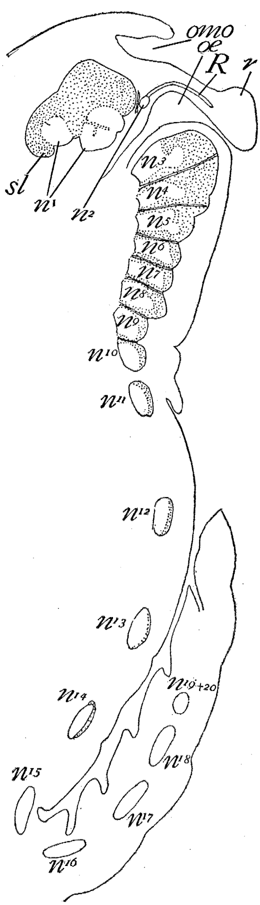
Stage 4. —(Fig. 4.) A glance at Fig. 4 will show that a piece is being constricted off of the posterior portion of each ganglion in segments eleven to fourteen and it will be seen in Fig. 5 that when the neuromeres begin to separate they do so at this newly formed constriction. In other words the posterior portion of one neuromere is constricted off and added to the succeeding neuromere. Patten supposed the neuromeres to be double, and used this fact, of which he was the first observer, to

support his view, comparing the process to a re-arrangement of pairs of neuromeres. But the parts that are displaced in the process are small masses of nerve tissue without nerves or cross-commissures and could not be regarded as neuromeres unless associated with separate segments of the body. This, Patten attempted to do, supposing the segments of all arthropods to be double, as shown by the frequent presence of "bifurcated appendages" and the "frequent occurrence of insect monsters having double pairs of legs." On the contrary my observations and reading lead me to believe that, with the exception of the diplopods (*Julus*), it is probable that the segments of all arthropods are single. In the scorpion embryo each segment except the first has one pair of mesoblastic somites and one pair of appendages.

The semilunar lobe (*sl*, indicated by a transverse band shaded slightly darker) has elongated somewhat and has moved upward and backward with the flexure of the anterior part of the neural band. In Figs. 5, 6, 7, 8 and 9 this process may be seen to continue until the anterior part of the nerve band is first perpendicular to the posterior or subenteric portion, and then by continued flexure bends backward. The ectoderm continues to grow over the first neuromere (*ec*). The mouth has continued to move backward, bending the œsophagus in the form of an arc (*æ*), compare Fig. 8, *æ*.

The appendages of the tenth segment are elongating to form the pectines, while those of segments eleven to fourteen have disappeared, their place being taken by lung books. Sterno-coxal processes, called maxillaria by Patten, have appeared on the fourth and fifth segments (*mx*).

Stage 5. — (Fig. 5.) In this stage the pits have almost entirely disappeared from the nervous tissue, being filled up by the growth of the cells composing their walls. The ectoderm has grown over the ventral chain, which has now become more compact. The nerves have begun to assume their definite form (4*A*, 4*P*), that is to say the peripheral nerve fibers are being compacted into nerves that can be distinguished in sections and sometimes in surface views. The ectoderm has grown further back over the head (*ec*). Pigment is beginning to appear in the median eyes.



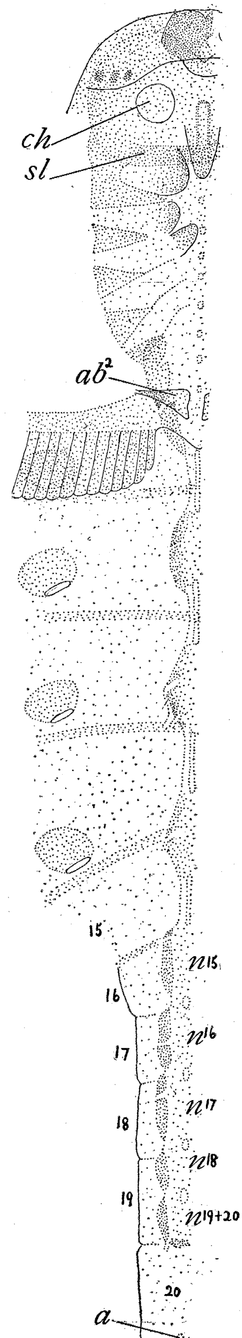


FIG. 8. Median sagittal section of an embryo of the seventh stage, $\times 45$; *œ*, œsophagus; *omo*, neck of median eye sacs; n^{1-20}, cross commissures of first to twentieth neuromeres; *r*, rostrum; *R*, rostral nerve; *sl*, semilunar lobe.

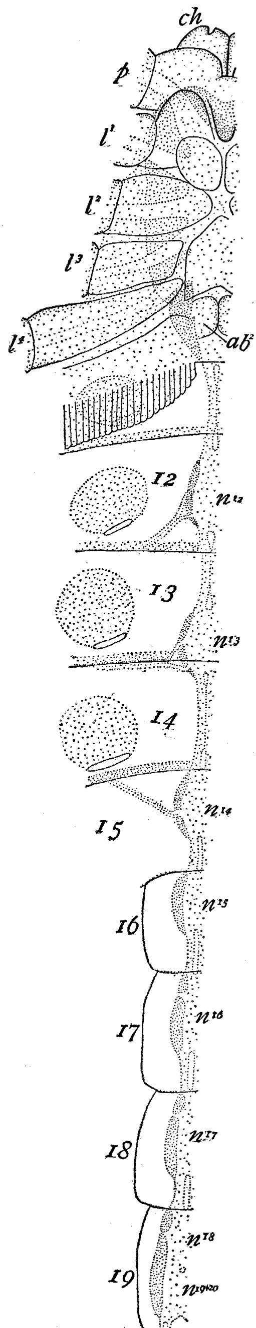
FIG. 9. Eighth stage of same, $\times 40$; *a*, anus; ab^2, second abdominal appendage; *ch*, cheliceral articulation; n^{15-20}, fifteenth to twentieth neuromeres; *sl*, semilunar lobe; 15-20, fifteenth to twentieth body segments.

Stage 6.—(Fig. 6.) The median-eye sacs have come together in the mid-line. In this stage I have worked out the nerves of the first thirteen neuromeres. Typically there are two pairs of nerves to each neuromere: an anterior pair ("hæmal" of Pat-

ten, "external" of Police) and a posterior pair ("neural" of Patten, "internal" of Police). In Fig. 6 the anterior nerves are shown in neuromeres four to thirteen (4–13, *A*) and the posterior nerves in neuromeres three to seven and nine to thirteen (3–7, 9–13, *P*). In the eighth segment the appendages have disappeared, and this may be the reason for the absence of the posterior nerves of this segment, which would normally innervate these appendages. The first neuromere has a pair of nerves that innervate the median eyes and a pair of nerves that innervate the lateral eyes. The second neuromere has a pair of nerves that innervate the chelicera and a median unpaired nerve that passes along the œsophagus to the rostrum. This rostral nerve may be a fusion of the anterior nerves of the second neuromere. The cheliceral nerves are serially homologous with the posterior nerves of the segments bearing walking legs. For the same reason I have called the single pair of nerves of the third neuromere posterior nerves. The twentieth neuromere is being drawn up into the nineteenth segment (*n* 20).

Stage 7. — (Figs. 7 and 8.) By a comparison of Fig. 7, which represents the nervous system as more or less transparent, with Fig. 8, which represents a median sagittal section of the nervous system with an outline of the ectoderm, I hope the reader may get a general idea of this stage of the embryo without the necessity of reading much description, and I will call attention only to special points.

The median-eye sacs have come together in the mid-line and open by a common neck (*omo*) to the exterior. Nerve-centers nineteen and twenty have completely fused. In the first neuromere there are two cross commissures, a fact which leads many to suppose that we have here two neuromeres, as does also the fact that it contains two pairs of optic lobes and two pairs of optic nerves. As to the optic lobes: Saint-Remy has shown that they are intimately associated by their nerve tracts. The significance of the optic nerves in relation to the segmentation cannot be determined here, as they cannot be homologized with anterior or posterior nerves of succeeding segments, for, on the one hand, it is doubtful whether their end organs represent appendages and, on the other hand, their roots cannot be traced to the ventral or



central columns of Police, as these columns cannot be distinguished in the first neuromere.

Stage 8. — (Fig. 9.) The changes that have taken place since the preceding stage are slight, and may be easily seen by comparing Figs. 7 and 9. It may be noted that the fifteenth nerve center has shifted to the sixteenth segment, the seventeenth nerve center to the eighteenth segment, and that the eighteenth, nineteenth and twentieth nerve-centers lie in the nineteenth segment.

Stage 9. — (Fig. 10.) This represents the embryo at the time of birth. The definitive outer form has been attained but the ganglia are proportionally larger

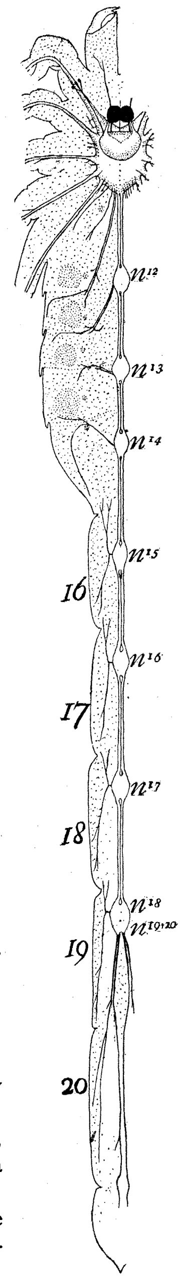


FIG. 10. Ninth stage (at the time of birth), × 34. Drawn with the camera lucida from two cleared preparations, and compared with dissections and series of sections. ab^2, second abdominal appendage forming the genital opercula; *ch*, chelicera; *p*, base of pedipalp; l^{1-4}, bases of walking legs; n^{12-20}, twelfth to twentieth neuromeres; $^{12-19}$, twelfth to nineteenth body segments.

FIG. 11. Tenth stage (adult), × 7. Camera lucida drawing of a dissection from the dorsal side. n^{12-20}, twelfth to twentieth nerve centers; $^{16-20}$, sixteenth to twentieth body segments.

than in older individuals. A further displacement of nerve centers results in that of the fourteenth segment being located in the fifteenth.

Stage 10. — (Figs. 11–13.) This is the adult stage, and since there is little change in the nervous system after the first moult, except increase in size, it will apply equally well to young or old individuals.

I have not been able to add anything to the excellent work of Saint-Remy and of Police (1901, 2) concerning the internal structure of the nerve centers. The nervous system of the

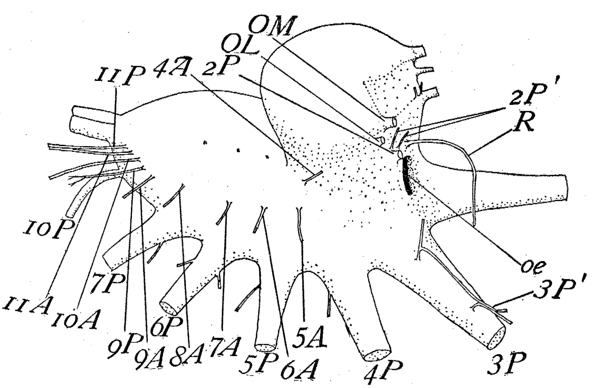


FIG. 12. Tenth stage (adult), × 34. Drawn from a plastic model of the cephalothoracic nerve mass made with the aid of dissections and series of sections in three planes. *OL*, lateral eye nerve; *OM*, median eye nerve; *R*, rostral nerve; $2P$, cheliceral nerve; $2P^1$, branches of cheliceral nerve; $3P$, pedipalp nerve; $3P^1$, branches of pedipalp nerve running parallel a short distance; 4–$11A$, anterior nerves of neuromeres four to eleven; 4–7, 9–$11P$, posterior nerves of corresponding neuromeres.

scorpion has been dissected and figured by many skilled observers, but in the light of my observations on the embryology perhaps I may call attention to some facts of interest.

Each cheliceral nerve (Fig. 12, $2P$) gives off two small branches ($2P^1$) just before piercing the outer neurilemma. Patten figures two small nerves in this position which he calls the "anterior and posterior hæmal nerves" of this neuromere, but from a study of their development I feel certain that they are merely branches of the cheliceral nerve.

Patten describes and figures a large ganglion in connection with a branch of the pedipalp nerve and a branch of the "anterior

hæmal" nerve of the same neuromere. What he calls the "anterior hæmal" nerve is another branch of the pedipalp nerve. I have carefully studied the nerves in the region where he described the ganglion (Fig. 12, $3P^1$) but have been unable to find the ganglion.

The nerves to the thoracic appendages and the pectines are larger, and arise from a more ventral part of the cephala-thoracic nerve mass than the other nerves and are classed by Patten as "neural" nerves. Fig. 12 shows how I have classified these nerves from a study of their development better than a description would do. In Fig. 11 I have shown that neuromeres eleven to

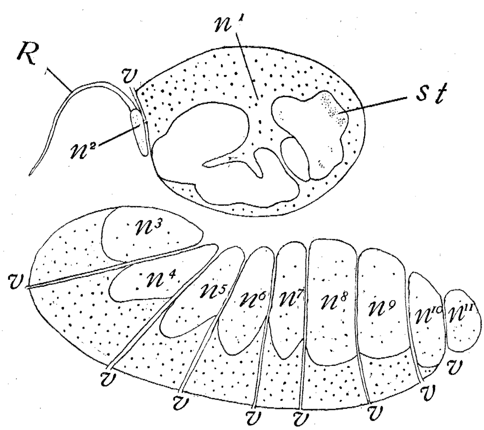


FIG. 13. Tenth stage (adult), × 34. Median sagittal section of cephalothoracic nerve mass. n^{1-11}, first to eleventh neuromeres; *R*, rostral nerve; *st*, stratified organ of Saint-Remy; *vv*, blood vessels between the neuromeres.

twenty innervate not only their corresponding segments, but each sends nerves to muscles lying in the succeeding segment. It is possible that the myomeres as well as the nerves are displaced somewhat backward. Patten claims that in the scorpion some nerves wander to segments to which they did not originally belong, and describes certain nerves (Fig. 12, 9*A*, 9*P*, 10*A*, 11*A*, 11*P*) as "vagus" nerves. Police (1901, 1) denies that this is true, and with the exception stated above, it is not true according to my observations.

Summary of Results.

In the scorpion there are twenty neuromeres, corresponding to the twenty body segments (not considering the telson as a segment).

The type of neuromere in the early embryo consists of a pair of ganglia fused in the mid-line and two pairs of nerves, anterior ("hæmal" of Patten "external" of Police) and posterior ("neural" of Patten "internal" of Police).

The first neuromere departs strikingly from the typical neuromere as the segment containing it departs from the typical segment. The second neuromere has no anterior nerves unless they have fused to form the rostral nerve. The third neuromere has no anterior nerves. The eighth neuromere has no posterior nerves. The remaining neuromeres are typical.

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